arnoldia

The Magazine of the Arnold Arboretum

ANEMONE VIII.

Groene Ridder.

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Volume 63 • Number 1 • 2004

Arnoldia (ISSN 004–2633; USPS 866–100) is published quarterly by the Arnold Arboretum of Harvard University. Periodicals postage paid at Boston, Massachusetts.

Subscriptions are $20.00 per calendar year domestic, $25.00 foreign, payable in advance. Single copies of most issues are $5.00; the exceptions are 58/4–59/1 *(Metasequoia After Fifty Years)* and 54/4 *(A Sourcebook of Cultivar Names)*, which are $10.00. Remittances may be made in U.S. dollars, by check drawn on a U.S. bank; by international money order; or by Visa or Mastercard. Send orders, remittances, change-of-address notices, and all other subscription-related communications to Circulation Manager, *Arnoldia*, Arnold Arboretum, 125 Arborway, Jamaica Plain, Massachusetts 02130–3500. Telephone 617.524.1718; facsimile 617.524.1418; e-mail arnoldia@arnarb.harvard.edu.

Postmaster: Send address changes to
Arnoldia Circulation Manager
The Arnold Arboretum
125 Arborway
Jamaica Plain, MA 02130–3500

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Page

Outside covers: The Arboretum's *Phellodendron amurensis* collection on Meadow Road photographed by Karen Madsen.

Inside covers: On the front, *Anemone* 'Groene Ridder'; on the back, *Rosa* 'L'admirable'; and below, a detail from *Caryophyllus florepleno*; all from *Hortus Nitidissimis* (see page 32).

Using Arboreta to Teach Biological Concepts

Foster Levy and Tim McDowell

Over fifty universities, colleges, and community colleges are listed among the members of the American Association of Botanical Gardens and Arboreta; an internet search uncovers many more campus arboreta, whether planted in discrete areas or dispersed throughout the campus. Biology teachers commonly use their arboreta for instruction in tree identification or to provide live material for studying plant morphology. In general, however, the myriad examples of evolutionary and horticultural diversity in these arboreta remain an underutilized resource. At East Tennessee State University we have successfully used arboretum-based activities to illustrate such biological fundamentals as species concepts, phylogenetic biogeography (the use of evolutionary relationships to infer the origin of current distribution patterns), and mutational genetic variation. The three

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KAREN MADSEN

Above is Magnolia x soulangiana *'Alexandrina',* M. denudata, *and* M. liliiflora. *The cultivar 'Alexandrina' is just one of many crosses between* M. denudata *and* M. liliiflora.

ALL BY PETER DEL TREDICI

Aesculus hippocastanum, A. *x* carnea, *and* A. pavia.

exercises described below should be of interest not only to biology teachers but also to anyone whose interest in trees goes beyond simply identifying and admiring them.

Exercise 1: What Makes a Hybrid?

Unlike animal hybrids, plant hybrids are common, they are often vigorous and sometimes fertile as well. Hybridization occurs both naturally, where species' ranges overlap,[1] and artificially, when plant breeders conduct crosses in hopes of combining the desirable characteristics of two or more lineages in a single plant. The highly popular saucer magnolia *(Magnolia* x *soulangiana),* for example, combines the early flowering characters of the Yulan magnolia *(Magnolia denudata)* with the purple flower color of the lily magnolia *(Magnolia liliiflora).* Other examples of parents and hybrids that thrive in a moist, temperate climate are listed in Table 1.

To demonstrate that species can maintain the capacity to interbreed even when their current ranges are widely separated and their morphological features have diverged widely, we use members of the genus *Aesculus* (buckeyes and horse chestnuts). In the southeastern United States, hybrids in this genus occur naturally in regions where ranges overlap,[2] and hybrids generated by controlled crosses have produced many horticulturally useful forms. The red horse chestnut *(A.* x *carnea),* a hybrid of the American red buckeye *(A. pavia)* and the eastern European horse chestnut *(A. hippocastanum),* is clearly a more showy and versatile landscape tree than either of its parent species, intermediate in size between them, and displaying a pink flower color that blends the deep scarlet and creamy white of the parents. Unlike most interspecific hybrids, individuals of *A.* x *carnea* are fertile, the result of a chromosome-doubling event in the hybrid lineage that permits all chromosomes to pair with its homolog and thereby complete the meiotic cell division that precedes gamete formation.[3] (Most hybrids have single chromosomes and are therefore unable to reproduce.)

Buckeyes and horse chestnuts are particularly useful examples for classroom study because the identities of the parents as well as the hybrids can be deduced from bud and twig characters; this frees the teaching module from seasonal dependence and eliminates the need for mature specimens, although when present, flowers and fruits provide a wealth of additional evidence for the hybrid origin of the red horse chestnut. Another advantage is that both the red horse chestnut and one of its parents, the red buckeye, flower and fruit when small and relatively young (three to six years of age); and although sterile and therefore fruitless, the other parent, the double-flowered horse chestnut cultivar (*A. hippocastanum* cv. 'Baumanii'), may also flower when very small.

At the beginning of the exercise, students receive basic instruction in the morphology of

FOSTER LEVY

Branches with terminal buds and leaf scars of horse chestnut (left), red horse chestnut (center), and red buckeye (right). Note parental differences and hybrid intermediacy in bud size, bud-scale coloration, bud stickiness, leaf-scar shape, and twig diameter.

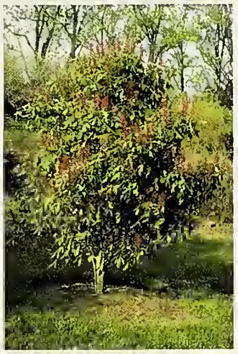
flowering plants—leaf types, bud and flower structures—with particular emphasis on the characteristics that delineate the genus *Aesculus:* opposite, palmately compound leaves; large, scaly terminal buds; flower or fruit characters, if present. They are then shown four tree specimens and told that two are parent species A, one is parent species B, and one is a hybrid of A and B. (We use two rather than one representative of one species to illustrate the relative constancy of distinguishing characters.) Working in small groups, students learn to distinguish the parent species from the hybrid by looking for the intermediacy between parental features that most hybrids show. Each group then constructs a taxon/character matrix for use in discussing their conclusions with the entire class. The taxon/character matrix in Table 2 highlights some of the easily observable differences among the three taxa of *Aesculus*.

When leaves and/or flowers are available, we also teach the students how to determine whether the fertile hybrid species *A.* x *carnea* is a polyploid—that is, whether it has more than two copies of each of its chromosomes. A high proportion of species of modern flowering plants owe their origin to hybridization

Table 1. Examples of parent-hybrid combinations suitable for planting in USDA zones 5–8.

Common Name	Genus	Parent A	Parent B	Hybrid
Buckeye	*Aesculus*	Red buckeye *A. pavia*	European horse chestnut *A. hippocastanum*	Red horse chestnut *A.* x *carnea*
Witch hazel	*Hamamelis*	Chinese hazel *H. mollis*	Japanese witch hazel *H. japonica*	Many named selections *H.* x *intermedia*
Magnolia	*Magnolia*	Lily-flowered magnolia *M. liliiflora*	Yulan magnolia *M. denudata*	Saucer magnolia *M.* x *soulangiana*
Viburnum	*Viburnum*	Korean spice viburnum *V. carlesii*	Chinese snowball *V. macrocephalum*	Fragrant snowball viburnum *V.* x *carlcephalum*
Sweetshrub	*Calycanthus*	Carolina allspice *C. floridus*	Chinese sweetshrub *Sinocalycanthus chinensis*	Raulston allspice x *Sinocalycanthus raulstonii*
Sycamore	*Platanus*	Eastern sycamore *P. occidentalis*	Oriental planetree *P. orientalis*	London plane *P.* x *acerifolia*
Locust	*Robinia*	Black locust *R. pseudoacacia*	Bristly locust *R. hispida*	Casque rouge locust *R.* x *margaretta*

Table 2. Comparison of traits in the hybrid red horse chestnut and its parents, the American red buckeye and the European horse chestnut.

	Red Buckeye *(A. pavia)*	**Red Horse Chestnut** *(A. x carnea)*	**Horse Chestnut** *(A. hippocastanum)*
			
Natural range	southeast U.S.	garden origin	Albania, Greece
Stature	small tree (<20')	medium tree (20–40')	large tree (>100')
Landscape use	small yards	yards, streets, parks	parklands
Leaf characters			
Leaf blade	flat	slight slope	"ski jump" slope
Leaf teeth	fine	medium	coarse
Leaf color	deep green	green	yellow-green
Leaf gloss	glossy	varies by selection	flat
Leaf texture	smooth	often strongly wavy	slightly wavy
Bud/twig characters			
Leaf bud color	tan	brown	dark brown
Leaf bud scales	smooth	lightly sticky	very sticky
Leaf scar base	shallow, obtuse "U"	rounded "V"	deep, acute "V"
Twigs	flexible, thinner	less stout	stiff, straight, very stout
Flower characters			
Flower color	scarlet red	pink	creamy white
Flower throat	long (>1")	short (<1")	short (<1")
Flower tip	narrow	flared	flared
Petal spot	small, yellow	showy yellow	faint
Fruit characters			
Capsule husk	smooth	small prickles	stout prickles
Seeds/capsule	1 to 2	1 to 3	2 to 4
Genetics			
Chromosomes	40	80	40
Fertility	fertile	fertile!	fertile

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followed by polyploidization to restore fertility. Polyploid plant species often have significantly larger stomata and pollen grains than their diploid relatives. Indeed, some polyploid species have been shown to have stomata that are more than fifty percent wider in diameter than those of their diploid relatives,[4] but no comparisons have been reported for *A.* x *carnea* and its parents.

To investigate the question, students prepare a section of the lower leaf epidermis from each parent species (both diploids) and from the hybrid, *A.* x *carnea* (a tetraploid, which has four sets of chromosomes); then, using a simple eyepiece scale bar on a compound microscope at 100 to 400x magnification, they measure stomate diameters for each taxon's leaves and compare averages. If flowers are available, they measure pollen sizes in the same way after preparing wet mounts of pollen. Compared to related diploid species, pollen of polyploids is often twenty percent wider in diameter.[5] A survey of pollen in the horse chestnut family (Hippocastanaceae) reported slightly larger pollen diameters (three to ten percent greater) for the polyploid *A.* x *carnea* compared to the largest pollen grains from the parental species.[6]

Exercise 2: Morphological Variation Within a Species

Although biology curricula emphasize the principle that natural selection shapes populations by acting on variations arising from mutations, examples of actual mutations in multicellular living organisms are seldom provided in the classroom. Students therefore have little opportunity to assess the range of morphological variations that exists within a single species. In contrast to biologists, horticulturists actively seek out and propagate naturally occurring, rare variants, using selective breeding to develop more extreme forms. An exercise that bridges the intellectual divide separating the disciplines of horticulture and biology can help students develop an appreciation for the range of observable variation and at the same time introduce them to two other topics in evolutionary and systematic biology: character correlations and evolutionary parallelisms.

The arboretum on our campus, like most, includes specimens of the typical ("natural") form of many species in addition to artificially generated horticultural selections of the same species. We give our students a map showing the locations of several forms of a species and ask them to document the traits that distinguish them from each other. An example is the sawara false cypress *(Chamaecyparis pisifera)*, a large species (more than 65 feet, or 20 meters, tall) native to Japan that is now common in our cultivated landscapes. In the typical form, needles are scale-like, pointed, and arranged in flat green sprays. In contrast, the cultivars *C. pisifera* cv. 'Plumosa' and *C. pisifera* cv. 'Squarrosa'—both large trees—have softer and more pointed leaves, respectively. The 'Boulevard' cultivar (*C. pisifera* cv. 'Cyano-viridis') is a small tree (10 to 30 feet, or 3 to 10 meters, tall) whose needles are soft and bluish. Smaller, "bun-shaped" selections, some with variegated foliage, are often grown in dwarf conifer gardens or used as foundation plantings. This series of species and cultivars allows students to observe mutant forms that encompass wide variations in leaf coloration, positioning, and texture, and a range in height from tall through smaller to extreme dwarfing.

After surveying and describing the variations, the students construct a hypothesis to explain their rarity in natural populations. One hypothesis might be that selection acts against dwarfs or plants that are deficient in chlorophyll (as evidenced by their lighter-colored foliage). Chlorophyll is crucial to survival because it mediates the conversion of the sun's energy into plant sugars.

Next, with their lists of characteristic traits in hand, students are asked to judge which traits seem to be correlated, as opposed to occurring independently. In the *Chamaecyparis* examples, we look for relationships between pairs of observed variant characteristics, i.e., between color and texture, between color and size, and between size and texture. It is well known that correlations among characters can act as a constraint on evolution, but students are seldom given firsthand views of these correlations .[7] In *Chamaecyparis* and other taxa, leaf variegation is often correlated with small stature. The reduction in chlorophyll (evidenced by the white/yellow leaf coloration) limits the plant's

photosynthetic capacity and growth potential. Hence, strongly variegated individuals are usually small plants.

In another variation of this exercise, each student group analyzes a different species group to address the question of whether similar variations occur in unrelated species. If so, the reason may be evolutionary parallelism—variations caused by parallel, but independent, mutations in different species. Once again, leaf variegation provides an instructive example. The variegated phenotype (outward appearance) can be caused by mutations in several different genes. These mutations are not uncommon and they are found throughout the world of green plants, in ferns, gymnosperms, monocots, and dicots.

Within the angiosperms, the genus *Ilex* (the hollies) is a good source of examples of intraspecific variation. *Ilex* cultivars present a fantastic array of remarkable traits selected by horticulturists. Variegated leaf forms display contrasting patterns of yellow, white, and green. Leaf spines may be totally absent, or few and marginal, or abundant on margins and extending into the middle of the leaf. The varied and distinctive growth habits within *Ilex* include narrow columnar forms, contorted forms, and extreme dwarf forms.

Besides demonstrating a broad range of mutational variations, the hollies provide lessons on floral and reproductive biology. Because most hollies are dioecious (unisexual), most cultivars are also either female (having berries) or male (bearing pollen). At the ETSU Arboretum we have planted dozens of cultivars of dwarf evergreen hollies together with our dwarf conifers, providing a tremendous diversity of forms within a small outdoor space.

It is not difficult to develop a small collection of intraspecific forms. Nurseries now carry dozens of cultivars of sawara false cypress, of

Leaf variation in cultivars of the sawara false cypress (Chamaecyparis pisifera). *Note differences in leaf size, density, position relative to the twig, disposition around the twig, and flexibility. A fruiting cone appears above 'Plumosa'.*

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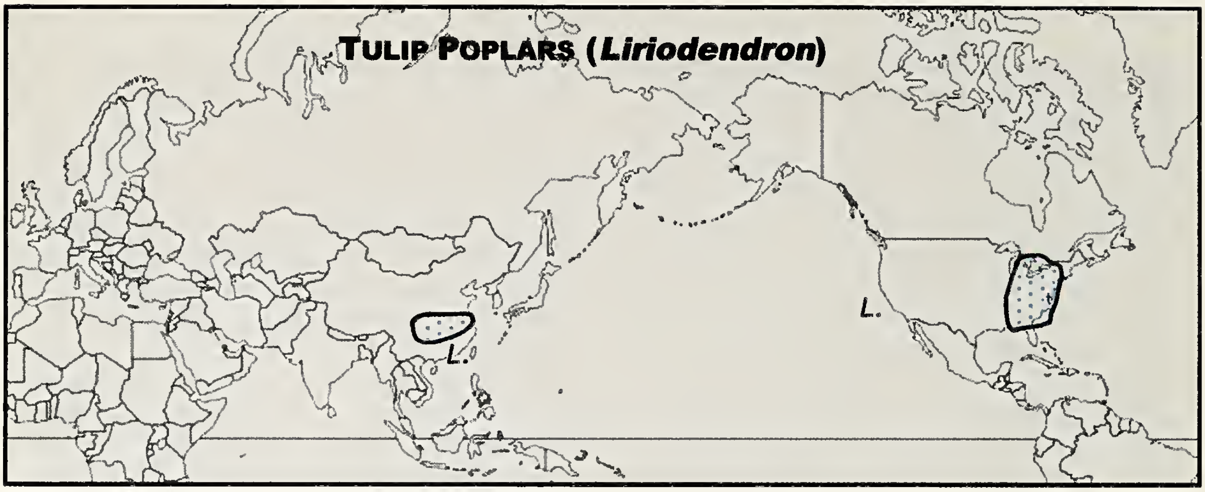
	'Plumosa'	'Squarrosa'	'Cyanoviridis'	'Green Snow'	'Minima'
Height	tall (>20 m)	tall (> 20 m)	medium (< 10 m)	short (<6 m)	dwarf (< 1 m)
Leaf Density	very dense	very sparse	sparse	dense	sparse
Leaf Position	appressed	spreading	spreading	tips spreading	spreading
Leaf Length	short	long	long	short	medium
Leaf Texture	firm	stiff	soft	firm	stiff
Leaf Color	green	blue-gray	blue	green	blue



Ranges of the American and Chinese tulip poplars.

Japanese cryptomeria *(Cryptomeria japonica)*, and of the evergreen American and European hollies *(Ilex opaca* and *I. aquifolium)*. Evergreen species are useful in allowing these exercises to be conducted throughout the year, but representatives of common deciduous species may be added to demonstrate the highly diverse horticultural variants of flowering dogwoods, red maples, and crabapples. At the Arnold Arboretum, plantings of wild and cultivated forms of *Cercis canadensis* (redbud) will help fulfill the educational goals of the Leventritt Garden.

Exercise 3: Biogeography of Asian-American Disjunct Distributions

The evolution of new species has often resulted from extreme climate change or geological processes like continental drift. The extraordinarily broad spans involved in space and time are difficult to grasp, but clear evidence of these remote processes exists in geographically separated pairs of related plant species. A hands-on view of these pairs, known as "vicariants," provides vivid proof that species inhabiting different continents may be closer relatives than species of the same genus that live near one another.

The closely related floras of eastern North America and East Asia comprise one of the most thoroughly documented examples of vicariant species. The disjunct distribution of these evolutionary "sister species" has fascinated botanists for over 250 years.[8] A continuous temperate flora is believed to have covered much of North America, Europe, and Asia during the Tertiary, 16 to 65 million years ago. The present-day distribution of temperate deciduous forests reflects several dramatic changes that occurred in subsequent periods. Climatic shifts diminished the range of suitable habitat, and glaciations caused species migrations and extinctions. Most important for understanding the relationships between the floras of East Asia and eastern North America, however, were changes in sea level that severed intercontinental links. At the ETSU Arboretum, we have several side-by-side plantings of sister species that illustrate the results of this history, as does the Arnold Arboretum's Leventritt Garden.[9]

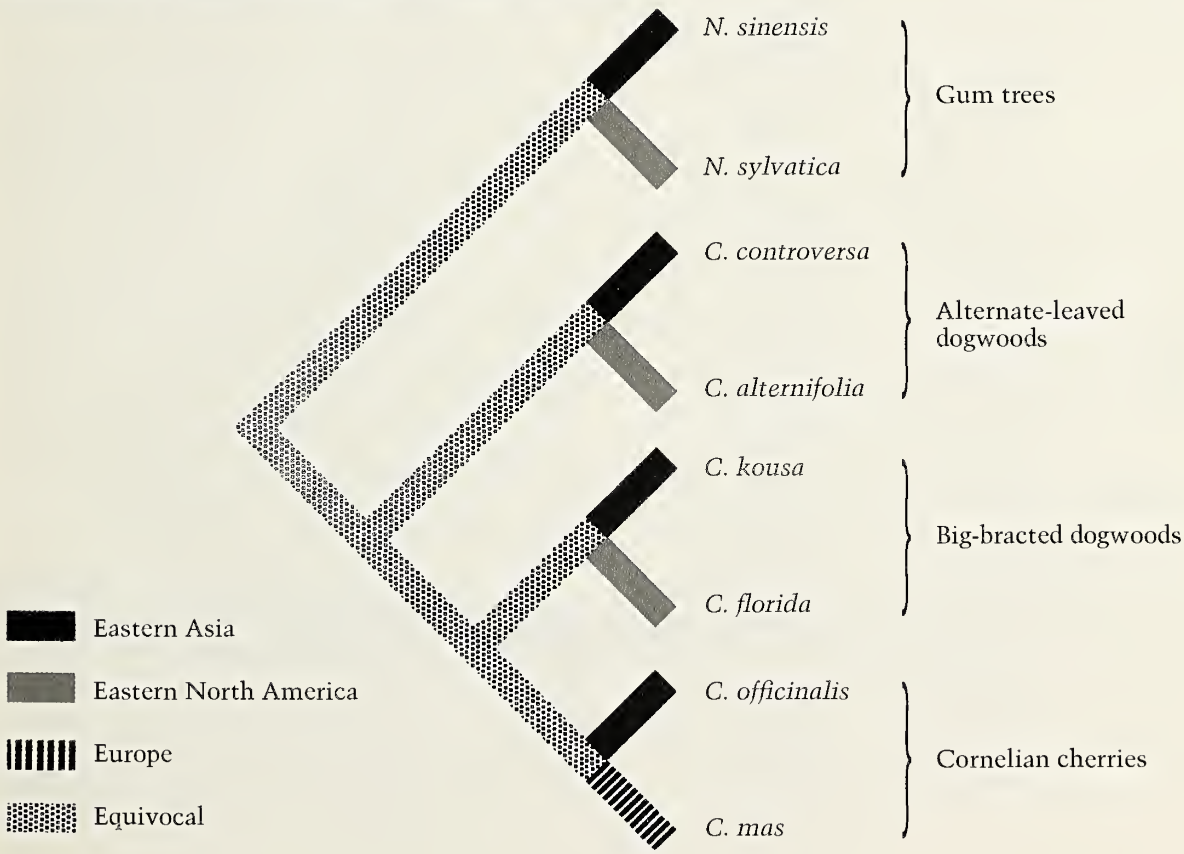
Students in our classes study the morphology of live specimens of these species and then construct a phylogenetic tree—a diagram showing evolutionary relationships among the species. Our investigation of intercontinental disjuncts begins with a discussion of the two species in the *Liriodendron* genus of the magnolia family, the widespread eastern American tulip poplar *(L. tulipifera)* and its closest relative, the Chinese tulip poplar *(L. chinense)*, a species with a narrow distribution in central China. After defining the differences and similarities in the vegetative morphology of the two species, students are given a species distribution map and a phylogenetic diagram—a family tree—of the entire magnolia family to demonstrate the close evolutionary relationship of the two tulip poplars.

Students then collect the morphological data needed to perform their own phylogenetic anal-

ysis on other pairs of disjunct species, three pairs from the genus *Cornus* (dogwood) and one from *Nyssa* (gum trees), both in the order Cornales. Each genus has representatives in both eastern Asia and eastern North America, but *Cornus* also includes representatives native to western North America and Europe. Although flowering material is preferred, vegetative characters such as leaf arrangement and bud scales are also informative; in any case, reproductive characters of many dogwood species are on view much of the year because fruits persist from summer into winter and flowers are available in early spring.

Within *Cornus,* one intercontinental grouping is made up of the big-bracted species, a group that includes the well-known flowering dogwood *(C. florida)* native to the eastern United States and its Chinese counterpart, the kousa dogwood *(C. kousa)* as well as the western flowering dogwood *(C. nuttallii),* native to the Pacific states. Another sister-species relationship includes the eastern American alternate-leaved dogwood *(C. alternifolia)* and the East Asian giant dogwood *(C. controversa),* the only two species in the genus with alternately arranged leaves. The European cornelian cherry *(C. mas)* and its closest relative, the Japanese cornel *(C. officinalis),* demonstrate the European-Asian historical connection through their similar umbellate inflorescences with four non-showy bracts and yellow flowers that appear before the leaves. Within the genus *Nyssa,* the close relationship between the widespread eastern American black gum, or tupelo *(N. sylvatica),* and the East Asian gum *(N. sinensis)* is revealed by scaly, ovoid, terminal buds; axillary flowers; and single, dark-blue, stone fruits. Students invariably uncover the sister-species relationships linking the pairs of

Phylogenetic tree (based on morphological data collected by students) showing relationships and distribution of selected species in *Cornus* and *Nyssa.*



big-bracted species and alternate-leaved species, cornelian cherries and gums.

With their firsthand knowledge of the taxa and the phylogenetic diagrams they have drawn, students can then refer to the scientific literature, either in libraries or on the internet, and compare their diagrams to those generated by experts who analyzed both morphological and molecular characters.[10] This exercise not only enhances students' awareness of the morphological bases for defining species but it also demonstrates vividly the concept of descent of species from a common ancestor.

Many native tree species besides those in *Cornus* and *Nyssa* demonstrate the East Asian-eastern North American distribution; Table 3 lists other pairs of vicariant sister-species growing in our campus arboretum. More exhaustive lists can be found in Li and Wen.[11] Examples of vicariant pairs are also available for western North America[12] and Europe.

Logistics

The benefits of an established campus arboretum are obvious, but if none is available, these exercises can be conducted with a lim-

Table 3. Examples of East Asian–eastern North American disjunctions. Number of species are shown for each region.

Family	Genus	Common name	Eastern N.A.	East Asia	Outliers
		ANGIOSPERMS			
Bignoniaceae	*Catalpa*	Catalpa	2	4	4 (Caribbean)
Caprifoliaceae	*Diervilla*	Bush honeysuckle	3		
	Weigela	Weigela		10	11
Fabaceae	*Cladrastis*	Yellowwood	1	4	—
	Cercis	Redbud	1	5	2 (w. N.A., Eur.)
	Gymnocladus	Coffeetree	1	4	—
Hamamelidaceae	*Hamamelis*	Witch hazel	2	2	—
	Liquidambar	Sweetgum	1	3	—
Illiciaceae	*Illicium*	False anise	3	37	2 (Caribbean)
Juglandaceae	*Carya*	Hickory	15	2	—
Lauraceae	*Lindera*	Spicebush	2	58	—
	Sassafras	Sassafras	1	2	—
Saxifragaceae	*Itea*	Sweetspires	1	9	—
Styracaceae	*Halesia*	Silverbell	3	1	
	Styrax	Snowbell	2	many	many (SE Asia; SA)
		GYMNOSPERMS			
Cupressaceae	*Chamaecyparis*	False cypress	1	3	2 (w. N.A.)
	Thuja	Arborvitae	1	2	1 (w. N.A.)
Pinaceae	*Tsuga*	Hemlock	2	6	2 (w. N.A.)

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From left, Rhododendron *'P.J.M.',* R. minus (= R. caroliniana), *and* R. dauricum. *'P.J.M.' is the result of a cross between the two species.*

ited number of plants, including many of small or dwarf stature that are inexpensive and can be confined to a relatively small area. A minimum of just three plants is required for the hybrid exercise, four for the variation exercise, and two or three pairs for the intercontinental disjuncts exercise. At an average of 25 dollars a plant, the entire suite can be obtained for less than 300 dollars. We recommend that plants be purchased from local nurseries to avoid shipping costs, but excellent mail order sources are available for harder-to-find specimens, including Arbor Village (arborvillagellc.com), Forestfarm Nursery (www.forestfarm.com), Greer Gardens (www.greergardens.com), and Woodlanders Inc. (www.woodlanders.net). Unlike a collection of multicellular animals, a small collection of hardy woody plants needs no day-to-day care, and long-term maintenance requires only occasional mulching, fertilizing, and pruning, as well as watering during droughts. Woody plant collections are thus ideally suited for hands-on investigations into variation, hybridization, and phylogenetic descent.

Endnotes

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PETER DEL TREDICI

The two Liriodendron *species,* L. chinense *at left,* L. tulipifera *at right, and their hybrid,* L. tulipifera x chinense *'Chapel Hill', between them.*

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Acknowledgments

We thank the Tennessee Department of Agriculture Urban Forestry Program and the Stanley Smith Horticultural Trust for financial support, the U.S. National Arboretum, the J. C. Raulston Arboretum, Highland Creek Nursery and Holly Haven Nursery for donations of plants, and E. S. Walker for helpful comments on the manuscript.

Foster Levy, Ph.D., a population geneticist, and Tim McDowell, Ph.D., a plant systematist, are both associate professors in the Department of Biological Sciences at East Tennessee State University. Dr. Levy's research has examined the genetic basis of hybrid sterility among species of *Phacelia* (Hydrophylaceae). Dr. McDowell has studied relationships among New World species of *Exostema* (Rubiaceae). They co-founded the ETSU Arboretum, making particular use of their southern Appalachian Mountain climate to emphasize elements of the East Asian and eastern North American floras.

In Favor of Trees

John Brinckerhoff Jackson

LIKE millions of other Americans I have no great liking for wilderness and forest, but like the majority of Americans I am fond of trees: individual trees, trees in rows along the street or in orchards, trees in parks. I continue to plant them when and where I can—to such an extent that when their leaves start to fall I look forward to many months of raking and transplanting in preparation for the spring.

The value of trees is not only that they can be beautiful and that they give us shade and privacy and coolness in the summer; they also demand our attention and care. We are constantly interacting with trees: some of them give us fruit, others give us firewood, and all have to be thought about and even worried about when we consider the future. In brief, trees give us a sense of responsibility and sometimes a kind of parental pride; each domesticated tree calls for an individual response, a response far richer, far more rewarding than a strictly passive—aesthetic or ecological—response to the forest.

What geographers call the Atlantic landscape stretches across northwestern Europe—England, France, the Lowlands, Germany, and Scandinavia; and in the course of the last three centuries it has been transplanted to Canada and the United States. It can be thought of as the gradual creation of those Indo-European migrants who came out of Asia some seven thousand years ago with their livestock and who eventually occupied all of Europe. In addition to the Atlantic landscape north of the Alps, they also produced the Mediterranean landscape—equally varied and beautiful, but adjusted to a mountainous terrain, hot dry summers, and no great abundance of moisture. By contrast, the Atlantic landscape—both in America and in the Old World—is characterized by a green, rolling topography with many rivers and plenty of rainfall. Mexico has a version of the Mediterranean countryside, and so have parts of New Mexico and California.

Century after century the early Indo-Europeans wandered from the Ukraine to Greece and Norway and even Ireland. When they occasionally settled down, their livestock grazed in the surrounding forests and grasslands, and families raised small crops of wheat or rye or barley. They brought with them out of Asia certain fruit trees. Alma-Ata, the capital of Kazakhstan, means "father of apples," for the mountains in that part of Central Asia once contained immense forests of nothing but apple trees, as well as forests of pear trees and apricot trees. Those fruit trees, as well as certain nut trees, were greatly prized by the migrants, for

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they provided sugar and oil, as well as calories, and when planted (or transplanted) they symbolized the permanent home and family.

The forest was, of course, the dominant element in that prehistoric landscape—even the landscape of what we used to call the Dark Ages: the period between the fall of Rome in the fifth century A.D. and the Norman Conquest of England six hundred years later. It was a frightening and inhospitable place, extending from Poland on the east all the way (with numerous breaks, to be sure) to Holland—which, paradoxically enough, means "land of woods." We hear much about the density and extent of the Amazonian rainforest, but one of the largest and most impenetrable forests in the world is in northern Russia, of which it is said no one knows what fear is who has not been within its dark and tangled precincts. Nowhere was the early forest looked upon with anything but awe. Legend depicted it as the habitat of giants and elves and mythical creatures, a refuge for outlaws and dangerous spirits; and some of that legend persists in familiar fairy tales.

Nevertheless, the forest played an important role in peasant economy. It provided firewood, wood for building, and a variety of herbs and wild fruits; cattle from the village grazed in the grass-grown clearings, and under the many oak trees herds of pigs ate acorns and mast. Cultivation in the forest was forbidden, and the small stockman, the small farmer was largely dependent on the garden, the common grazing land, and on the trees planted by the family or the village.

One of the attractive features of the Atlantic landscape in the Middle Ages was its popular culture based on wood: the planting and care of trees which produced fruit or provided material for a great number of crafts. The forest still contained much oak, the most prestigious of trees; but the open landscape, the landscape of fields and meadows and houses and gardens, contained an increasing variety of fruit trees imported from elsewhere; trees whose wood could be used for household needs and for wagons and plows; trees which, because of their everyday importance, eventually acquired symbolic value.

In the book *Sylva*, the seventeenth-century Englishman John Evelyn mentions an old German law which stipulated that "a young farmer must produce a certificate of his having set a number of walnut trees before he have leave to marry." Since the smelting of iron threatened in the seventeenth century to destroy many English forests, Evelyn suggested that what he called "iron mills" be established in New England. "'Twere far better," he wrote, "to purchase all of our iron out of America than to exhaust our woods here at home."[1]

Sylva, originally in four volumes, is an encyclopedia of arboriculture as practiced in pre-industrial Europe. Evelyn tells how to collect and plant the seed of numerous "useful" trees, when and where to plant, how to protect, trim, and feed them, and how finally to cut them and process the wood. Though the oak remained the king of trees—Evelyn devotes twenty pages to describing and praising it—he has much to say about each of the others:

> Elm is a timber of most singular use, especially where it may be continually dry, or wet, in extremes; therefore proper for water works, mills, the ladles and soles of the wheel, pipes, pumps, aqueducts, ship planks below the water line . . . also for wheel-

wrights, handles for the single handsaw, rails and gates. Elm is not so apt to rive [split] . . . and is used for chopping blocks, blocks for the hat maker, trunks and boxes to be covered with leather; coffins and dressers and shovelboard tables of great length; also for the carver and those curious workers of fruitages, foliage, shields, statues and most of the ornaments appertaining to the orders of architecture . . . And finally (which I must not omit) the use of the very leaves of this tree, especially of the female, is not to be despised . . . for they will provide a great relief to cattle in the winter and scorching summers when hay and fodder is dear. . . . The green leaf of the elms contused [crushed] heals a green wound or cut, and boiled with the bark, consolidates fractured bones.[2]

In reading Evelyn, we discover two kinds of pleasure. One comes from reading a wonderfully idiomatic English, clear and unaffected, emphasizing the visible, tangible everyday aspects of his topic. The second comes from many glimpses of a vernacular, country way of life based on the skillful exploitation of a local resource: the growing and cultivation and processing of trees used for making houses and furniture, in home remedies, in food and liquor and cooking; trees planted in farm gardens, in orchards, along country roads, in clusters to provide shade for cattle, trees in stately double rows to mark the avenue leading to a noble mansion, or to a town; each with its own traditional value to the craftsman, the artist, the housewife, the builder. Many retained from the remote past a powerful symbolism. The linden or lime tree was the tree of justice, local courts being held in its shade; the yew and the cypress symbolized immortality, and the apple tree stood for domesticity: so much so that a French geographer suggests that the apple tree is a prime symbol of the Atlantic landscape, just as the olive tree symbolizes the landscape of Mediterranean Europe.[3]

Evelyn wrote his book because of his concern over the increasing scarcity of certain essential types of wood. The king's navy and the growth of transatlantic commerce threatened the English supply of oak. Foundries and mills and furnaces consumed more and more forest wood, and the needs of a growing urban population for fuel, as well as the destruction of many forests in wartime, all threatened the existing stands. *Sylva* was accordingly addressed to the great landowners of England, urging them to plant as many trees as possible in a wholesale manner. It should be noted that Evelyn nowhere recommends the traditional forest of mixed woods, the hunters' forest. What he advised, not only for England but also for the Continent, was the creation of systematic, commercial forestry; and that was the type of forestry which evolved in the eighteenth century.

It was in the English colonies in North America that the old vernacular culture of trees was given a fresh lease on life. The early settlers lost little time before destroying (for commercial use as well as for clearing land for farming) immense areas of virgin forest. That, in fact, is what had happened to the forests of medieval Europe, but in America—again as in Europe—the planting and cultivation of trees flourished as never before. For that is a distinction we must always make: the forest as a massive collection of trees of all varieties is seen as a resource, not as an environment. Whereas the single or planted tree is seen by most of us as a permanent, carefully tended element of the human landscape, valued as an object both of beauty and of sustainable exploitation.

In any case, colonial America found several new ways of using trees. We developed an improved type of ax, the water-powered sawmill, and learned to build houses and bridges and dams and even roads entirely out of wood. Following the example of the native Indians, colonists extracted sugar from maple trees. Early in colonial history, we undertook to plant trees along our streets and roads, for shade and shelter, and when independence came, many towns and villages celebrated the event by erecting liberty trees. When the Midwest was settled

in the early nineteenth century, immigrant handbooks and other periodicals advised the settlers to plant orchards first of all, even postponing the planting of a vegetable garden.

We soon had plenty of food on the market, and plenty of wood was still available in the forests. So the culture of trees in America took a new turn: trees were planted chiefly for their beauty and symbolism. Starting in New England in the 1850s, where women's organizations were dedicated to the beautifying of towns and cities, a national enthusiasm for ornamental trees everywhere transformed the village square, the college campus, many country roads and graveyards. The landscaped cemetery composed of winding roads, groups of trees, and expanses of lawn was in a sense the reconstruction of the old pre-industrial landscape of legend. On the treeless prairie the farmhouse was surrounded by a grove of trees, and their bright autumn colors gave certain trees an almost symbolic value, unique to America.

This widespread cult of ornamental trees brought about an immense increase in the number of nurseries and tree farms. At the same time, the nation as a whole became increasingly aware of deforestation in many regions. Beginning more than sixty years ago, at the time of the Great Depression, state and federal government agencies launched vast programs of tree planting. Hundreds of thousands of saplings were planted to check erosion, to break the force of the wind, to provide habitats for wildlife, to control flood waters, to modify the climate. Millions of trees, whole forests, were planted for ecological reasons.

Two generations ago the word *ecology* was rarely heard, and to most Americans the very notion that forests—natural or artificial—could serve other than human needs was a revelation. I am old enough to have lived through those first large-scale ecological experiments, and in retrospect I think we generally approved of them—though there still lingers among Americans the ancient belief that the forest is there for us to exploit in the meeting of daily needs: for fuel, for food, for grazing, for hunting, and for escape from social restrictions. The national park or forest is still thought of in terms of recreation and camping, and to be reminded of the many ecological benefits of the forest simply confirmed the reality of that prehistoric prototype. As a result, those numerous planted groves and belts and forests were quickly assimilated into the landscape and their recent origin forgotten. In fact, many of the windbreaks have been destroyed—or harvested—by farmers totally unaware of their original purpose.

It could be said that the reforestation or tree-planting programs of the Depression years helped inaugurate the environmental movement in this country. In that sense they were part of a worldwide shift in attitude toward the natural environment. Here for the first time on an extensive scale, the landscape, or part of it, was being deliberately altered not to serve immediate human needs but to preserve the natural order. It is quite true that in the course of planting and reforestation many highways were landscaped, many rest areas and recreational facilities came into being. It is also true that our national parks, even when overrun with visitors,

try to make us feel that as citizens we are inspecting one sample of our national estate. Nevertheless, our national and state parks actually provide us with only the faintest reminders of our earlier forest or wilderness experience.

The contemporary forest experience emphasizes the *visual* aspect, the scenic, the ecological, the photogenic. We are not to touch, much less pick up and carry away, any object we find of interest. We are tactfully told that we are not at home but in a museum; a museum, moreover, which is increasingly concentrated on ecological or geological or botanical phenomena. The risk of vandalism and destruction helps justify this hands-off policy, though the influence of current environmentalist policy—the determination to preserve nature totally undisturbed by man—has had its effect. For the fact of the matter is, humanity's closest and most productive relationship with nature derives from personal, physical contact, and from a desire to appropriate whatever attracts us. "Leave nothing behind, not even footprints," the environmentalists advise those of us who go into the wilderness. "Take nothing except photographs." The visual experience, the spectator experience, is the only one permitted.

Our true feeling for trees derives from an ancient source—from centuries of domesticating, improving, protecting, and loving those other forms of life which are part of our daily existence. Looking back over more than half a century, I am struck by our growing desire for trees in our domestic environment, by our desire to plant trees, regardless of their economic value, in order to express a variety of basic emotions: the need to celebrate the home, the need for beauty, the need for some living thing to protect and transform, the need to pass on to the future some sign of our existence. Ecologists encourage us in this enthusiasm, assuring us that the tree we plant will help cleanse the atmosphere, moderate the climate, and close the gap in the ozone layer. But John Evelyn, nearly 350 years ago, provided us with a better justification: "Men seldom plant trees until they begin to be wise; that is, till they grow old and find by experience the prudence and necessity of it . . . 'Tis observed that such planters are often blessed with health and old age." He added, in a passage I take very much to heart, "I am writing as an octogenarian, and shall, if God protract my years, and continued health, be continually planting till it shall please him to transplant me to those glorious regions above, the celestial paradise—for such is the tree of life, which those who do his commandments have right to."

Notes

[1] John Evelyn, *Sylva: or a Discourse of Forest Trees* (1664; London, 1679), 118.

[2] Ibid., 114, 20.

[3] Daniel Faucher, *Géographie agraire: Types des cultures* (Paris: Librairie des Médicis, 1949).

John Brinckerhoff Jackson (1909–1996), a geographer by training, was a pioneer in the field of landscape studies. He founded *Landscape* magazine and taught the history of the vernacular American landscape at Harvard University and the University of California, Berkeley.

A Good Day: Plant-Collecting in Taiwan

Rob Nicholson

One of the greatest plant hunters of the last hundred years was E. H. Wilson, an Englishman who spent years in East Asia collecting plants for the nursery trade and for the Arnold Arboretum. Thanks to his perseverance, thousands of plants were introduced into cultivation in the United Kingdom and the United States. Since Wilson's six collecting trips to Japan, China, Korea, and Taiwan, many botanists have covered the same ground that he did, often using his maps and books as guides for re-collecting the plants he found there. The tales of his collecting adventures often spark envy in latter-day plant collectors like me: Wilson got there first, and he got there when the hunting was far better.

The thick forests Wilson bushwhacked his way through are being overrun by human populations, and some of the species he collected are now endangered and possibly extinct in their former habitats. Of the eighteen genera and twenty-four species of conifers known in Taiwan, for example, the Red List of Threatened Plants of the IUCN (International Union for Conservation of Nature and Natural Resources) classifies twelve species as vulnerable, rare, or endangered. One has only to look at before-and-after satellite photos of the last twenty years to realize that within the next hundred years the world's forests will be reduced to the weeds and scraps left behind from a once great cornucopia.

Wilson's first visit to Taiwan began in January 1918. From his ship rocking on the waves of the Pacific Ocean off the eastern coast of the island, he could see the 7,000-foot mountains meet the water's edge, leaving only the narrowest strip of beach or coastal plain, if any at all. The small boat that took him into shore was manned by "half-breeds of Chinese and savages [who] work the boats ashore, yelling as loudly as possible all the time. They maneuver the boat so as to get it carried stern first on the crest of the wave well to shore. As the wave recedes one jumps ashore and races to safety." Wilson's party included botanists and soldiers from Japan, which then ruled the colony called Formosa. The soldiers had been brought along to fight off mountain tribes that were said to practice headhunting. It is a measure of Taiwan's remarkable economic explosion that eighty years later the only headhunters in evidence are of the corporate variety.

Taiwan was a plant hunter's paradise in Wilson's day and much of it remains so today. Its mountains rise to over 13,000 feet (the highest between the Sierra Nevada Mountains of California and the Himalayas) and harbor lush conifer forests and alpine plants on their flanks and summits. Most of the terrain is so steep that landslides are frequent; development in regions other than the western coastal plain is therefore minimal. So rugged are the interior mountains that only three roads connect the east and west sides of the 244-mile-long island. At lower altitudes an intergrading mix of temperate, subtropical, and tropical floras grow, with a number of species endemic to Taiwan. Taiwan is particularly rich in gymnosperms, the cone-bearing plants such as conifers and cycads. Wilson collected twenty species in fourteen genera of gymnosperms. Among the most remarkable is the massive conifer taiwania *(Taiwania cryptomerioides)*, which rivals the redwoods and giant sequoias for size.

> The taiwania, named for the island, is the loftiest tree in the forests, rearing its small, mop-like crown well above its neighbors. The average height of this tree is from 150 to 180 feet but specimens exceeding 200 feet are known. The trunk is sometimes as much as 30 feet in girth, quite straight and bare of branches for 100 to 150 feet. It is a strikingly distinct tree, singularly like a gigantic club moss or lycopod. In the dense forests the crown is small, dome-shaped or flattened, the branches few and short, and

A riverside Taxus chinensis*—the sole survivor of a stand of nine.*

> one wonders how so little leafage can support so large a tree. When the top is broken by storms, the lateral branches assume an erect position. In the more open forest the branches are massive, widespreading, with an oval or flattened crown. On small trees the branches [are] often pendant. When young it is singularly beautiful in habit of growth.

Wilson brought back seven herbarium collections of taiwania as well as a few young trees from which cuttings were propagated and distributed in the United States. One propagule was given to Pierre S. du Pont (1870–1954) of Longwood Gardens in Pennsylvania, and he passed it along to the Fairmount Park of Philadelphia. Paul Meyer of the Morris Arboretum, however, tells me that no taiwanias are known to exist in the Philadelphia area today.

Beginning in 1997 I undertook a series of collecting trips to Taiwan myself, often following in Wilson's footsteps and, like him, concentrating on conifers and cycads. A number of the plants I wanted to collect contain powerful chemical compounds that pharmaceutical trials have shown to be useful against various cancers and leukemias. Other species on my target list were rare and endangered; one, *Amentotaxus formosana,* is on the IUCN's shortlist of the planet's sixty most rare and endangered conifers. Many institutions worldwide are attempting to establish *ex situ* collections of these highly endangered plants to prevent their total extinction.

On my most recent trip, the second in the series, I collaborated with Shu-Miaw Chaw of the Academia Sinica Taipei, a specialist in the molecular genetics of gymnosperms, who would be collecting DNA samples from various species. The pleasures of hunting for plants in a tract of unspoiled forest are many: every few yards the landscape gives up another treasure or another mystery, making the forest seem like an enigmatic box of wonders. However, finding desired plants in the vast green mosaic of a forest canopy is not the easiest of occupations. This expedition, like most, involved both the joys and the miseries of collecting in the wild.

On the first day of our expedition, we headed up Taiwan's western coast, the wide plain that faces the Taiwan Strait and that supports the vast majority of the island's human population. Our group included Dr. Chaw, three of her students, and me. Many of the plants on our target list were in the yew and plum yew families, of which Taiwan boasts a great number: *Taxus chinensis, Cephalotaxus wilsoniana,* and the rare *Amentotaxus formosana* can be found in its forests. The latter two genera grow throughout Southeast Asia but occur only sporadically and never, to my knowledge, in large populations.

Our first collections were of the Chinese yew, *Taxus chinensis,* known for the powerful anticancer taxane compounds like taxol and bac-

Overleaf: On the eastern coast of Taiwan 7,000-foot mountains drop straight into the water. All photographs are by the author.

catin III that are found in its bark and needles. A stand that Dr. Chaw had seen on previous trips now consisted of a single tree. We were told that eight trees had been illegally harvested within the last year, probably for sale in Japan, where yew-wood desks bring exorbitant sums from business executives. We continued driving through the rain to 7,800 feet, our driver clearly uneasy about landslides. I was stunned by the giant *T. chinesis* we next stopped at, a stout colossus eighty feet high with a trunk that measured eight feet in diameter—the largest yew I have ever seen in my collection trips around the world.

On our target list for the second day was a plum yew named for E. H. Wilson, who was the first to bring specimens out of Taiwan: *Cephalotaxus wilsoniana* (Wilson's plum yew), named by Japanese taxonomist Bunzo Hayata (1874–1934). While similar to yews in appearance, plum yews belong to a different family and have very different chemical compounds. Its foliage can be mistaken for yew, but it has much larger fruits, held in clusters, and its seeds are entirely enclosed by the fleshy aril. Chinese researchers have isolated a number of chemicals from *Cephalotaxus* that show promise in treatments for granulocytic and myelocytic leukemias; Western pharmaceutical researchers have also shown interest in it. Of the six to eight species known, *C. wilsoniana* is the only one considered endangered, so we wanted to collect the species both for its rarity and its efficacy.

On the day we planned to search for *Cephalotaxus wilsoniana,* we left Taipei in the usual Taiwanese drizzle, our highway winding past blocks of gray, factory-like apartments that sprouted beneath the lush green hills. Ornately painted temples with upcurved corners provided the only refreshment for the eyes in this soggy urban landscape. The road wound upward, switchback after switchback, frequently passing scars from past landslides; in one area an entire village had been covered.

At 4,600 feet we entered the YuShan National Park and soon began to see conifers, among them pine, spruce, and hemlock. After parking at the highest point of the road, 8,456 feet, we walked into a restricted research area, a rich forest with a dense understory of ferns and forbs beneath towering conifers, including some Morrison's spruce that were six feet across and 150 feet high. Where slides had occurred, thick brambles of roses and blackberries had sprouted. We bushwhacked through the trackless forest, looking for the stand of plum yew that was said to be there, but after hours of fruitless hand-to-thorn combat we surrendered. The effort was not a total loss, however, since I collected a beautiful plant of the lily family, *Polygonatum alte-lobata,* with large violet fruits dangling beneath the arching stem.

Cephalotaxus wilsoniana *seedlings.*

We drove on toward the Alisan National Scenic area, where Wilson himself had found *Cephalotaxus wilsoniana.* Spotting a large plum yew from the roadside, we clambered up a steep embankment of underbrush into the forest's dark and moist understory. *C. wilsoniana* abounded here, most of them with stems bent to horizontal and hanging over the steep slope. The largest had three trunks that com-

bined at the base to form a twenty-inch trunk. On a few female plants we found fruits, greenish drupes the shape and color of small olives. I knew from other species of *Cephalotaxus* that when the pulp is ripe, it has an amazingly heady aroma that in Taiwan attracts macaques to feed. Back at the roadside, Dr. Chaw and I divided the seeds and cuttings from two dozen trees, potential *ex-situ* collections for both our institutions. The day's successes were topped off by the sight of an endangered Mikado pheasant, *Syrmaticus mikado,* a black, white, and red beauty. We ended with an evening meal at a truckstop in Alishan, where Wilson had his base camp and where we also purchased plants of wasabi, the fiery oriental horseradish.

On the third day, our target was a member of the yew family (Taxaceae) that not even Wilson had collected in Taiwan, *Amentotaxus formosana* (Taiwan catkin yew). The genus *Amentotaxus* is comprised of only four to six species;

Foliage of Amentotaxus formosana, *the Taiwan catkin yew.*

and though found over a wide area in Southeast Asia, it is rare throughout. Two populations of *A. formosana* are known and accessible in Taiwan, and we planned to collect from both of them.

Our drive to the first location was halted abruptly by a fresh landslide. We could have dug our way through it, but a large boulder perched on the steep slope above persuaded us to backtrack quickly and head toward the second stand, farther north on the main coastal road. We cut eastward onto the craggy spine of the island along a typical mountain road: two parallel concrete strips to aim your tires at, with lush vegetation growing between them and on the sides. We passed gorgeous tropical gingers, *Alpinia speciosa,* and the curiously flowered *Mussaenda pubescens.* By the time we reached the boundary of the Amentotaxus Preserve, marked by a sign announcing its protected status, the day had become cloudy and dark with misty rain falling.

Setting out on the trail, we immediately spied examples of the beautiful ferns to be expected in this environment: two large tree ferns; another "miniature," eighteen-inch tree fern, *Diploblechnum fraseri*; epiphytic bird's-nest ferns resting on tree branches; and everywhere the fronds of numerous terrestrial ferns slowly waving in the mist.

Each specimen of *Amentotaxus formosana* in the preserve had been tagged and numbered, and we planned to take a few cuttings from as many as we could find. We thrashed our way through the fog into the forest, not knowing whether we had already passed by some of the trees we were looking for or even whether we were in the right area to find them. Each glance at our watches told us that dusk was approaching, and none of us relished the thought of navigating the twisting ribbons of road in the dark fog. There was little choice but to split up, with Dr. Chaw and her student Chih-Hui Chen heading down the slope and me covering higher ground.

As it grew darker our botanizing trek turned into a frenzy of activity, with all of us running along the fogbound trails, occasionally calling out for one another, desperately peering at the trees' darkening silhouettes in search of one particular shape and texture. After twenty

Botanist Shu-Miaw Chaw displays a hard-won branch of Amentotaxus formosana. *The author is at her right.*

minutes a muffled cry came from down the slope: they had found *Amentotaxus formosana.* I ran toward the cries, and we quickly took cuttings from as many trees as possible in order to get maximum genetic representation for the *ex-situ* collections.

Stopping for breath, we gazed at the trees stretching upward in the crowded forest, battling for light, their foliage as beautiful as that of any conifer I'd seen: seven-inch, dark green, stiletto blades marked on their undersides by pairs of dramatically white stomatal bands. Chih went farther downhill while Dr. Chaw and I collected cuttings and labeled each bag with the mother plant's identification number. The largest tree we saw was thirty-five feet high with a basal trunk diameter of eight inches, but Chih reported seeing a cut trunk fifteen inches in diameter farther down the slope. We managed to find twenty trees in the sliver of remaining light and then reassembled to hike back out to our vehicle.

Having failed to reach the first population and almost missing the second, we felt fortunate to have any collections at all for the day's effort. We packed up and bumped down the twin strips of concrete, our headlights illuminating the wild tangle of leaves and grass blades. We burst through the green dome of the forest and instantly found ourselves back in the urban sprawl of the coastal plain where we rewarded ourselves with a feast of shrimp, eel, and miso soup.

That night we pressed on around the bottom tip of the island and then up the Pacific-facing eastern coast to Taitung. Here the mountains come all the way down to the sea, leaving the area unpopulated and free of the stressful hustle of the western coastal plain. Our collecting goal for the next day was the one known population of *Cycas taitungensis,* the only cycad native to Taiwan. Cycads are remarkable organisms that defy our limited understanding of plants. Though most people guess them to be palms, they are gymnosperms, carrying naked seed that is held in a cone scale and not enclosed by a fleshy fruit. The fossil record shows cycad-like plants present in the early Permian Epoch,

Home of Cycas taitungensis. *At left, the narrow ravine of a whitewater river. Center, the cliffside path. Right,* C. taitungensis *on the ravine's slope.*

contemporaneous with the dinosaurs that were roaming around 250 million years ago. This was to be a first for me since I had never before collected a plant with so long a history.

In the morning we drove from the coast into the foothills along the course of the Lu Yeh River and began a four-mile hike up to the cycad population. At the lower elevations we passed through a lowland tropical rainforest, still glistening from the night's rain. One giant fern stood out, the epiphytic *Pseudodrynaria coronans* with its four-foot fronds, of which a specimen is now growing in the Smith College conservatory. An hour into the hike, we began to get sporadic glimpses of cycads in the forest shade, looking like old hermit gymnosperms in this forest of flowering trees. Chih spotted a cluster of germinating seedlings at the base of a tree, clear evidence of an animal or bird caching the seeds.

Dr. Chaw said the main stand was farther on, and another student, Shy-Yuan Hwang, pressed on alone; the rest of us followed after stopping for a snack. The path soon broke out of the forest into a sun-baked, rocky landscape through which a narrow gorge, 100 to 150 feet deep, had been carved through the shale by a whitewater river. We found hundreds of *Cycas taitungensis* in this short stretch, cliff dwellers perched atop the chasm or even growing on its sheer walls. Their habitat, a combination of extreme heat and dry rocky soils, is unusual in monsoon-soaked Taiwan but a niche that cycads occupy in many parts of the world.

So far we'd found none of the fecund females we were looking for, easily identified by their crowns of massive seed-bearing cones. We continued up the river valley, by now looking for the long overdue Shy-Yuan as well. The path began to deteriorate, showing few signs of use, and before long we came to a spot where a large rockslide of many acres had cut through the forest long ago, leaving the slope covered by a million plates of shale. We could see the trail winding over this heap of sliding, slippery shards and up the side of a sheer cliff, becoming a hand-carved half-tube 150 feet above the roaring rapids.

We all looked at one another. Had Shy-Yuan gone on? Numerous calls brought no answer. We decided that Dr. Chaw and I would go on while the others stayed and searched for seeds.

We threaded our way across the burning slate pile, sending an occasional rockslide to the river below, and finally reached the cliff path, which tilted toward the water so that we had to walk in a crouch, grabbing onto whatever roots and crannies we could. Any glance downward set my knees to wobbling. The trail curved, following the river, cutting into the cliff, and passing under some cliff-dwelling cycads—old Methuselahs anchored in the rock—and after the longest 100 yards of my life, it flattened out into the forest. The cycads soon disappeared, and we came to the obvious conclusion: Dr. Chaw's student would not have gone any farther. When our calls were met with silence we reversed our course. On our return, we found him with the rest of the group. The rapid-fire lecture that Dr. Chaw delivered to her wayward student was made only slightly less embarrassing by my ignorance of Chinese.

After lunch, I ambled down onto a bluff overlooking the river. A few dozen cycads grew there, some old eight-foot-long leaners and younger, upright umbrellas of five feet. And there, at the very edge of the cliff in full sun, stood a magnificent female *Cycas taitungensis,* its fifteen-inch-wide, minaret-shaped cone topping the trunk—a resplendent cluster of golden-furred cone scales with large, crimson, egg-shaped seeds.

A fifteen-inch fruiting cone of Cycas taitungensis.

Plucking seeds from the cone felt a bit like robbing eggs from a dinosaur's nest. The small number we collected would be used for germinating trials at our own institutions and for limited distribution to botanic gardens that specialize in *ex-situ* cycad conservation, such as Miami's Montgomery Center. (After six months in a seed pot, my seeds began to crack their thick coats and the first wisp of a leaf came curling up through the soil. It now graces our conservatory.) As we left the cycad valley, I thought to take a picture of Dr. Chaw, who was walking on the trail ahead of me. I readied my camera and just as I was going to call to her, she suddenly turned with a big smile and said, "This has been a good day." I clicked in agreement. Still alive, seed in the bag, a good day indeed.

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The Sex Life of the Red Maple

Richard Primack

Nature has carefully crafted the mating systems of plants and animals to insure genetic diversity in their offspring. Many plants, like some animals, occur as separate male and female individuals to make self-fertilization (which does not promote diversity) less likely. But beyond mere gender differentiation, plants have a wide variety of mating systems. In particular, members of the maple family, Aceraceae, are renowned for their diverse sexual systems; maples run the gamut of sexual reproduction. "Perfect" flowers—those with both stamens and pistils—occur in certain species, such as the Norway maple *(Acer platanoides)*. With perfect flowers self-pollination could occur if the plant's pollen reaches one of its pistils. Other species, such as the box elder *(Acer negundo)*, occur as separate male and female trees; the male trees' flowers have only stamens and the females' flowers only pistils. This separation of the sexes ensures that pollen must move between plants, ruling out self-fertilization.

Between these extremes, we find the especially unusual sexual system of the striped maple *(Acer pensylvanicum)*. Individuals of this species often form clumps of woody shoots that produce male flowers for a few years, followed by female flowers and fruit production for a few years, until the shoot dies. The rootstalk sometimes produces many shoots, each one going through this cycle, keeping the plant alive even though individual shoots die.

RICHARD PRIMACK

Observations were made in a swamp in Newton, Massachusetts. At this site the combination of surface rocks, standing water in winter, and dry conditions in summer limit the size of the trees. As a result, the flowers can be readily observed, and the trees bent over if needed for closer examination.

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A branch of red maple female flowers above and below a branch of male flowers. Flowers are produced in clusters of about five at nodes along the twig. Note the male flowers, which have long stamens extending beyond the red petals. In these older female flowers, the sides of the ovaries have already begun to take on the characteristic shape of the maple fruit and the stigmas have begun to wilt.

Botanists have long studied the reproduction of the red maple tree *(Acer rubrum),* but until recently there was no consensus on its reproductive biology. The red maple is an abundant, wide-ranging tree of moist woodlands and other habitats. It was described by the Harvard botanist M. L. Fernald (1873–1950) as being "polygamodioecious," meaning that some plants have just male flowers, others just female flowers, and still others have perfect flowers. P. Barry Tomlinson, professor at Harvard University, considered the plant to be "polygamomonoecious," a term indicating that a red maple plant may be entirely male, entirely female, or ambiguous in gender, producing both male and female flowers. Other terms have also been applied to the species. It is the unusual sexual system of the species that causes the confusion in terminology. Individual plants have behaved in perplexing ways: individuals that were thought by naturalists and homeowners to be male trees sometimes produced fruit. The problem was that no one looked at trees in detail over a long enough period to figure out what was going on. Such long-term monitoring is usually not undertaken by taxonomists, who are generally more concerned with developing methods for identifying and classifying species.

As a population biologist, I felt it was important to learn more about the reproductive biology of this common species. Starting in 1979, I monitored 79 small trees for the type and number of flowers that each produced as well as for other demographic characteristics. I checked plants carefully in 1980, 1982, 1983, 1984, and irregularly in subsequent years. All of the trees that I monitored inhabited a rocky, seasonally flooded swamp in which the red maples typically attain a height of only 6 to 30 feet (2 to 10m), allowing all of the flowers to be completely counted and the stems to be bent over for close inspection of flower types.

The site is located in the Hammond Woods, in Newton, Massachusetts, on the west side of the Hammond Pond Parkway. The maples here begin to flower between early and late April, as soon as the weather starts to get warm. The flowers, almost exclusively either male or female, are red to orange to yellowish in color, with five small sepals and petals. They are produced in bunches of about five, with all the flowers in a bunch being either male or female. Male flowers have long, extended stamens with abundant, dusty-yellow pollen and a reduced, nonfunctional pistil. Female flowers have a well-developed ovary, with two long stigmas and reduced, nonfunctional stamens. The length of the stamens and stigmas suggests that the plants are sometimes wind-pollinated, although the flowers are also visited by bees and other insects. Female flowers rapidly develop into flattened, winged fruits with zero, one, or two seeds. The fruits mature quickly and disperse by wind during the summer. Germination is rapid, and there seems to be no seed dormancy.

The 79 trees in my study fell into five gender categories. Fifty-three produced exclusively

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A close-up of two flowers, one female, on the left, and the other male. The stigma has begun to wilt in the female flower, and the pollen has been shed from the anthers of the male flower.

male flowers in every year of the study. Another six individuals were inconstant males, producing male flowers exclusively in most years but occasionally producing some female flowers. For example, for four years plant #28 produced only male flowers, but in 1980 it produced 46 male flowers and one female flower. Another plant produced male flowers in every year except 1979, when it produced 37 male and 137 female flowers. Most flowers from these inconstant male trees failed to develop into fruits, no doubt because the plants have a fundamental chromosomal abnormality that prevents fertilization or subsequent fruit development.

Twelve individuals were constant females, producing only female flowers in every year. Six were inconstant females, producing mostly female flowers in every year with some male flowers in one or more years. And of the 79 plants, two were highly variable in sexual expression, producing only male flowers in some years, only female flowers in other years, and mixtures of male and female flowers in yet other years. Overall, in a typical year the 79 plants produced a total of approximately 21,000 inflorescences of which 18,000 were male and 3,000 were female.

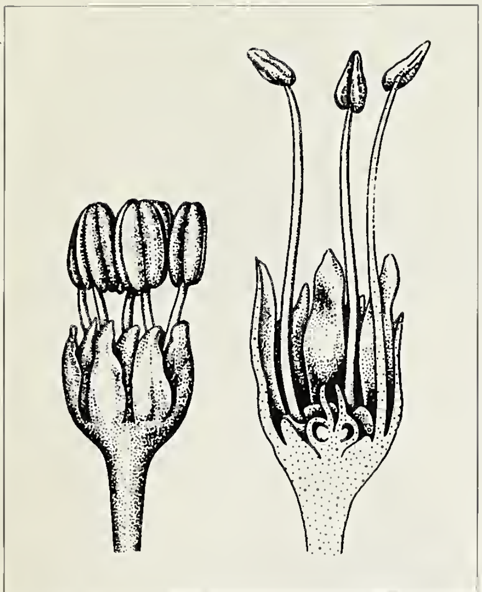
One year I enclosed the flowering branches of some trees in paper bags before they flowered to determine whether the plants were capable of self-pollination or required cross-pollination. All bags contained both male and female flowers. I cross-pollinated some of the bagged flowers using pollen from nearby trees, self-pollinated others using pollen from elsewhere on the same tree, and left others as unpollinated controls. Fruit set was over 90 percent in all three treatments, and most fruits had two seeds. This result indicates that the species is probably capable of automatic self-pollination since experimental self-pollination and cross-pollination did not improve fruit production.

Many of the trees at the study site had two or more stems coming from a common rootstock. In addition to the physical connection, the common origin of stems from a single plant could be identified by the distinctive color patterns of green, red, and yellow on the young leaves. In general, individual stems from the same rootstock confirmed the gender characteristics of the whole plant; that is, in constant male plants, all of the stems had only male flowers, while in constant female plants, all of the stems had only female flowers. However, in the inconstant and variable plants, some individual stems were very different from the others in some years. For example, in 1983 one inconstant female had four flowering stems with percentages of 10, 10, 70, and 83 female flowers, and in 1984 its remaining three flowering stems had percentages of 35, 86, and 89 female flowers.

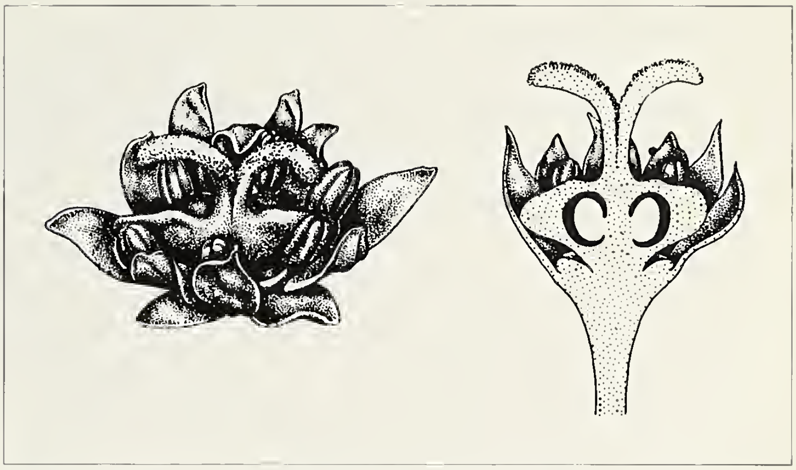
Growth and reproduction characteristics were compared across plants in the five gender groups. The most instructive difference was that constant female plants were more variable in flower production than were male plants. This makes sense biologically, as female plants producing large numbers of flowers in good years typically go on to produce large numbers of fruit and so may exhaust their energy reserves and be unable to flower well the following year.

Overall, the population is clearly bimodal in sexual expression. Male plants made up 75 percent of the population, 23 percent of the population were females, and 2 percent of the population varied in sex expression. However, of the 77 plants that could be clearly designated as either male or female plants, 12 plants were inconstant in gender and showed at least some evidence of producing flowers of the opposite sex. Such imprecision in dioecious species is known in other species as well; sometimes male plants make a few fruits and female plants

PRISCILLA FAWCETT. FROM THE SECOND EDITION OF P. B. TOMLINSON'S THE BIOLOGY OF TREES NATIVE TO TROPICAL FLORIDA, 2001



A male flower in side view and in longitudinal section at the stage of pollen dispersal. The long stamens are held out beyond the short petals. The ovary is small and undeveloped.



A female flower in side view and in longitudinal section, at the stage of pollen receptivity. Note the reduced, nonfunctional stamens and the short petals. The stigma has two branches and is at the top of the flattened ovary. The ovary will later develop into the characteristic maple fruit.

produce some male flowers. In this red maple study, individuals of both sexes could produce flowers of the opposite sex. Female plants had a greater tendency for variability than the males, with 33 percent of the females varying in sex expression whereas only 10 percent of the males varied in sex expression.

This study demonstrates the importance of checking for fruit production in investigations of plant gender. For example, inconstant males on occasion produced numerous female flowers, and so these plants were recorded as having some level of female fitness. Yet in some cases very few of the female flowers developed into fruits, indicating a genetic malfunction. Further, certain plants were recorded as having only male flowers even though subsequent checks showed that these plants produced some fruit. It is certainly easier in red maples, and probably in most other species, for a few inconspicuous female flowers to go unnoticed on an otherwise male tree than it is for a few of the conspicuous male flowers—with their strongly extended stamens and yellow anthers—to go unnoticed on an otherwise female tree.

Three unanswered questions remain: What is the genetic basis for the differences between male and female plants? Do all red maple populations include more male plants than female plants? Most important, how many years need a study last to determine these plants' complexities in gender expression?

More work is needed to determine what chromosomal and physiological mechanisms determine sex expression in red maples. More populations need to be studied to determine whether the results obtained in this one population of small individuals are applicable across the range of this widespread and variable species. Field work in this most useful next step in red maple studies requires only a pair of good binoculars, some way of marking or tagging individual trees, and a notebook. And last, studies of sexual expression in red maple need many years to complete. It is clear that a study of one or two years' duration would be inadequate for this species. Careful counting and patience over many years are needed to understand the otherwise confusing patterns of reproduction in this fascinating and ecologically important species.

Richard Primack is a professor at Boston University and a member of the Visiting Committee of the Arnold Arboretum. Along with several Boston University students, he has been conducting observations on flowering times at the Arnold Arboretum.

In the Library

Sheila Connor

***Hortus Nitidissimis Omnem Per Annum Superbiens Floribus Sive Amoenissimorum Florum Imagines*, or A year in a brilliant garden of exquisite flowers represented in beautiful pictures**

In September 2002, the Arnold Arboretum received a query from John Flanagan, librarian at the Royal Botanic Gardens at Kew, about our copy of *Hortus Nitidissimis,* one of the great florilegias of the 1700s. Because the *Hortus* was issued serially over a span of forty-two years (1750–1792), few if any extant copies are complete. In 2002, however, funding was provided by the Andrew W. Mellon Foundation to create a complete online *Hortus* by digitizing illustrations and text from copies held by the Natural History Museum, London, and the Royal Botanic Gardens. Because the Arboretum's copy includes ten plates (numbered 181–190) not found in either of the other two, these also became part of the "virtual" edition, and with the Arboretum's participation Kew was able to create an "Ideal Hortus," now online at www.kew.org/data/trew.

The extant copies of *Hortus Nitidissimis,* estimated to number fewer than twenty, vary widely since each of the engraved plates was hand colored, often by different artisans. The Arboretum's copy, accession number 16,641, is bound as a single volume rather than as three, as is the case with most. It was added to the library in October of 1907 through the generosity of the Skinner family, as attested by the bookplate, which states that the 22.10 pounds paid for the book to William Wesley and Sons, a British book dealer, came from Skinner funds. In 1904, Francis Skinner, a friend and neighbor of Charles Sprague Sargent, the Arboretum's first director, donated five thousand dollars for the "purchase of books for the Arnold Arboretum."

Skinner often volunteered at the Arboretum and for four months in 1880 had traveled with Sargent through the Far West, examining and comparing forests for the nation's tenth forest census. Early in 1907, Skinner's son, Francis Jr., contributed an additional five thousand dollars, suggesting that the books purchased with the money be considered a memorial to his father's interest in the Arboretum and its work.

Sargent used these donations frequently to order books, selecting many titles from Wesley's "Natural History and Scientific Book Circular." Excerpts from his orders and from the published Wesley catalog have occasionally been "tipped-in" to books that were purchased. A typed note tipped-in inside the cover of the *Hortus,* for example, states: "Trew, Hortus nitidissimis, the copy forwarded is more perfect than that in the Kew library, and has ten plates more than under Pritzel No. 9,500. Wesley [handwritten]." In fact, according to Stafleu and Cowan's *Taxonomic Literature,* the Arboretum's is the most complete set known to exist.

Kew's website includes a wealth of information about this great flower book, including a detailed history of its publication by W. J. Tjaden along with information about the physician and amateur botanist and horticulturist C. J. Trew, in whose garden the plants illustrated in the *Hortus* grew and who is often listed as its author. Of special value on the website is the translation of the *Hortus* into English. Readers can choose to view either the Latin transcription or its English equivalent, "which makes the rarest and most famous antique botanical books" accessible to a broad audience. Two of the Arboretum's ten singular illustrations are printed on the inside covers of this issue. The Arboretum's *Hortus* itself can be seen in the Horticultural Library in Jamaica Plain.

Sheila Connor is Horticultural Librarian and Archivist at the Arnold Arboretum.

ROSA XIV.

L'admirable

C.I.C. Wirsing jun. pinx. 183. *A.L. Wirsing Sc. et exc. Norimberg 1790.*